

## Discrete evolutionary color changes in caciques suggest different modes of carotenoid evolution between closely related taxa

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Carotenoid-based colors have signaling roles in a range of animal taxa, yet little is known about how carotenoids vary across species or whether overall patterns may vary across genera. The caciques (*Cacicus*, *Chypicterus* and *Ocyalus*; family Icteridae), a group of passerine birds from Central and South America, appear to visually divide into discrete yellow and red color groups. Reflectance spectrometry supported this observation, showing widely separated short and long-wavelength groups corresponding with yellow and red-feathered taxa. Ancestral state reconstructions inferred a yellow ancestral state with two independent changes to red, and no reversals back to yellow. This pattern contrasts with that of another closely related icterid clade, the New World orioles (*Icterus*), which exhibit a full range of carotenoid colors and have a pattern of evolution that is continuous and extremely labile. To our knowledge, this study is the first to highlight the possibility of different modes of color evolution even among closely related clades. This study also emphasizes the importance of the methods and assumptions of ancestral state reconstruction. In particular, although coloration and other characters can be measured along a continuous scale, they should be reconstructed using discrete methods when data from extant taxa and underlying mechanisms suggest discrete changes.

Carotenoid pigments produce a wide variety of elaborate animal colors including the lemon yellows, brilliant oranges, and scarlet reds found in many avian taxa (Brush 1990). Carotenoids, however, cannot be synthesized *de novo* by animals (Brush 1990). In birds the pigments may be deposited in feathers either directly or after being modified enzymatically to change their color, but ultimately they must be acquired through diet, usually from plants or arthropods (which derive their carotenoids from plants; Brush 1990, McGraw 2006a). Because they may be limited in the environment and costly to acquire, carotenoids in ornaments have potentially important roles in mating behaviour by possibly serving as an honest indicator of condition or foraging ability (McGraw 2006a, Hill 2006). Numerous experiments have shown that carotenoid plumage characteristics are related to sexual selection in a variety of avian taxa (reviewed in Hill 2002, 2006).

The New World blackbirds (family Icteridae) include many taxa with a wide variety of carotenoid plumage ornaments. Within this group the New World orioles (genus *Icterus*) are particularly diverse, with quantitative color data from extant taxa showing a full range of colors from yellow to red with multiple orange intermediates (Hofmann et al. 2006). Hence, Hofmann et al. (2006) reconstructed plumage coloration in orioles as a continuous

rather than a discrete character. In addition, plumage color is quite labile in orioles, showing multiple shifts from yellower to redder plumage and vice-versa (Hofmann et al. 2006). In many cases these changes have little correspondence with the relatedness of taxa, with several examples of drastic differences between sister taxa and surprising convergence between distantly related taxa (Hofmann et al. 2006). Overall, orioles show a continuous and highly flexible pattern of evolution in plumage coloration.

However, this pattern of color evolution does not seem to be representative of all birds, all passerines, or even all New World blackbirds with carotenoid colored plumage. Another group within Icteridae, the cacique clade (within the larger cacique and oropendola group) seems to show a very different pattern. Cacique taxa are found throughout Central and South America, and are diverse with respect to habitat, distribution, and life history (Jaramillo and Burke 1999). As adults, most taxa in this group have primarily black body feathers, but exhibit one or more patches of carotenoid-colored plumage, most often on the rump (Jaramillo and Burke 1999). These ornaments appear either yellow or red in adults of all taxa with obvious carotenoid coloration, and there seem to be no orange intermediates. This apparently discrete division between “yellow” and “red” color groups contrasts with the case of orioles, and

coupled with their close phylogenetic relation to orioles (Klicka et al. 2000), makes the caciques an interesting group for comparison. Another factor that makes the caciques a well-suited group for studying evolutionary patterns of coloration is the existence of a published, well-resolved molecular phylogeny onto which color can be mapped (Price and Lanyon 2004).

The possible discreteness of cacique coloration raises an interesting issue. Our method of measuring color, reflectance spectrometry, yields continuous data, and therefore makes it possible to reconstruct coloration as a continuous character (see Hofmann et al. 2006). However, if cacique color has evolved in discrete jumps rather than gradual shifts, reconstructing color continuously would be misleading in that it could show intermediately colored ancestors that did not exist. Therefore, it was important in this study to determine whether cacique color varies in a continuous or a discrete manner in order to generate an accurate reconstruction of ancestral states.

We had three main objectives in this study. First, we sought to use quantitative color measurements to examine whether cacique carotenoid coloration varies continuously or separates into discrete color classes. Reflectance spectrometry provides an unbiased and quantitative measure of coloration, which allows us to determine whether the separation of the “yellow” and “red” adult coloration is truly discrete. Second, we wanted to use these data to reconstruct color in the cacique clade to determine the directionality and number of changes in coloration throughout the cacique lineage. Finally, we wanted to compare the pattern of color evolution in caciques to that of orioles.

## Methods

### Selection and measurement of specimens

We used reflectance spectrometry to measure colored plumage patches of adult male museum specimens from the Smithsonian National Mus. of Natural Hist. and Field Mus. of Natural Hist. collections. Our study focused on a clade (hereafter referred to as the cacique clade) within the larger cacique-oropendola group from Price and Lanyon’s molecular phylogeny (2002, 2004). This clade includes two taxa previously considered oropendolas that were recently shown to be more closely related to caciques (*Clypacterus oseryi* and *Ocyalus latirostris*) and excludes two *Cacicus* taxa (*C. melanicterus* and *C. solitarius*), that would make the caciques paraphyletic if included here (Price and Lanyon 2002, 2004). *C. koepckeae*, an extremely rare species, was excluded altogether from both this study and Price and Lanyon’s (2004) phylogeny because specimens were unavailable.

We measured three to five individuals from each of the twelve recognized taxa of the cacique clade (Sibley and Monroe 1990, Jaramillo and Burke 1999, Price and Lanyon 2004). In monotypic species with large ranges, we attempted to sample individuals from as wide a geographic distribution as possible. The rump is elaborately colored in most taxa of the cacique clade, and is often the largest colored region (see illustrations in Jaramillo and Burke 1999). Therefore, we concentrated on this plumage patch.

In two taxa carotenoid coloration was not present on the rump but was present elsewhere on the body – specifically, on the tail (*Clypacterus oseryi* and *Ocyalus latirostris*). In these cases we used measurements from the dorsal surface of the tail. We are confident in this direct comparison between rump and tail because, in taxa that had more than one plumage patch, all colored areas yielded nearly identical measurements (unpublished data). However, to ensure that our findings were not significantly influenced by the treatment of these taxa, we also scored them as black and as missing data (see below).

We followed methods previously described in Hofmann et al. (2006) using a USB 2000 reflectance spectrometer (Ocean optics), and full-spectrum light source (providing both visible and UV illumination) to obtain reflectance spectra. Measurements were standardized against a diffuse white standard (Spectralon) and the dark, and were taken perpendicular to the plumage patch. Spectra were measured from 300–700 nm to include the full avian visual range (Hart 2001), and five non-overlapping replicates were taken from the relevant body region of each individual. The spectra were binned into one-nanometer increments using a custom-designed computer program (THC CMH and TWC unpubl. data), and the replicate measures for each individual were averaged.

### Defining color characters

We used spectral location, a descriptive colorimetric variable that most closely corresponds to hue, to define character states (Andersson and Prager 2006, Montgomerie 2006, see also Hofmann et al. 2006). Spectral location (or  $\lambda R50_{vis}$ ), is the wavelength at the point where reflectance is halfway between its minimum and maximum – i.e., the reflectance midpoint. We used spectral location to define color because, while it is quantitative and independent of the biases of any particular visual system, it is still relevant to how color is perceived (Hailman 1977, Andersson and Prager 2006, Hofmann et al. 2006). To humans, shorter wavelength spectral locations correspond to yellower colors, while longer wavelengths appear redder. Spectral location was calculated for each individual, and then measurements were averaged for each taxon. Three character states were defined using the resulting values. Coloration was defined as “yellow” for taxa with average spectral locations between 510–540 nm, and “red” for those with spectral locations between 580–600 nm. If a taxon had no visible colored plumage, it was defined as “black” (achromatic). However, because of the ability of melanins to mask the presence of carotenoids (e.g., Hofmann et al. 2007), it was not possible to differentiate between the loss or masking of carotenoids. Therefore, we also treated black taxa as missing data.

### Reconstruction of color

We used Price and Lanyon’s previously published phylogeny of the caciques and oropendolas to reconstruct evolutionary changes in cacique coloration (2004). This phylogeny is based on sequence data from two mitochondrial genes, cytochrome b and ND2 (Price and Lanyon 2002, 2004). We reconstructed color as a discrete,

unordered character using both parsimony and maximum likelihood (Schluter et al. 1997) in Mesquite (Version 2.5; Maddison and Maddison, 2008). For maximum likelihood reconstructions, branches were scaled according to molecular distance. To allow a more direct comparison with our previous work in orioles, we also reconstructed color as a continuous character using linear parsimony (Hofmann et al. 2006).

## Results

### Color data

Spectra from all colored taxa yielded distinct carotenoid-like reflectance curves, with low reflectance at shorter wavelengths, a sharp increase at middle wavelengths, and a high-

reflectance plateau at longer wavelengths (Fig. 1; also see examples in Bleiweiss 2005, Shawkey and Hill 2005, Hofmann et al. 2006, Andersson and Prager 2006). The curves of “yellow” taxa also had a small secondary reflectance peak in the UV (300–400 nm; Fig. 1). These peaks are common in carotenoid-based plumage and are artifacts of the subtractive nature of carotenoid colors (Shawkey and Hill 2005, Andersson and Prager 2006). Their presence or absence does not affect our measure of spectral location. We found no evidence for melanin-based colors, which lack the distinct plateau of carotenoid-based colors (McGraw 2006b, Hofmann et al. 2007).

To the human eye, cacique colors appear as discrete “yellow” and “red” plumage groups. Both the general shapes of the reflectance spectra and the quantitative spectral location data support this observation (Fig. 1). Spectral location values also fell into two separate groups.

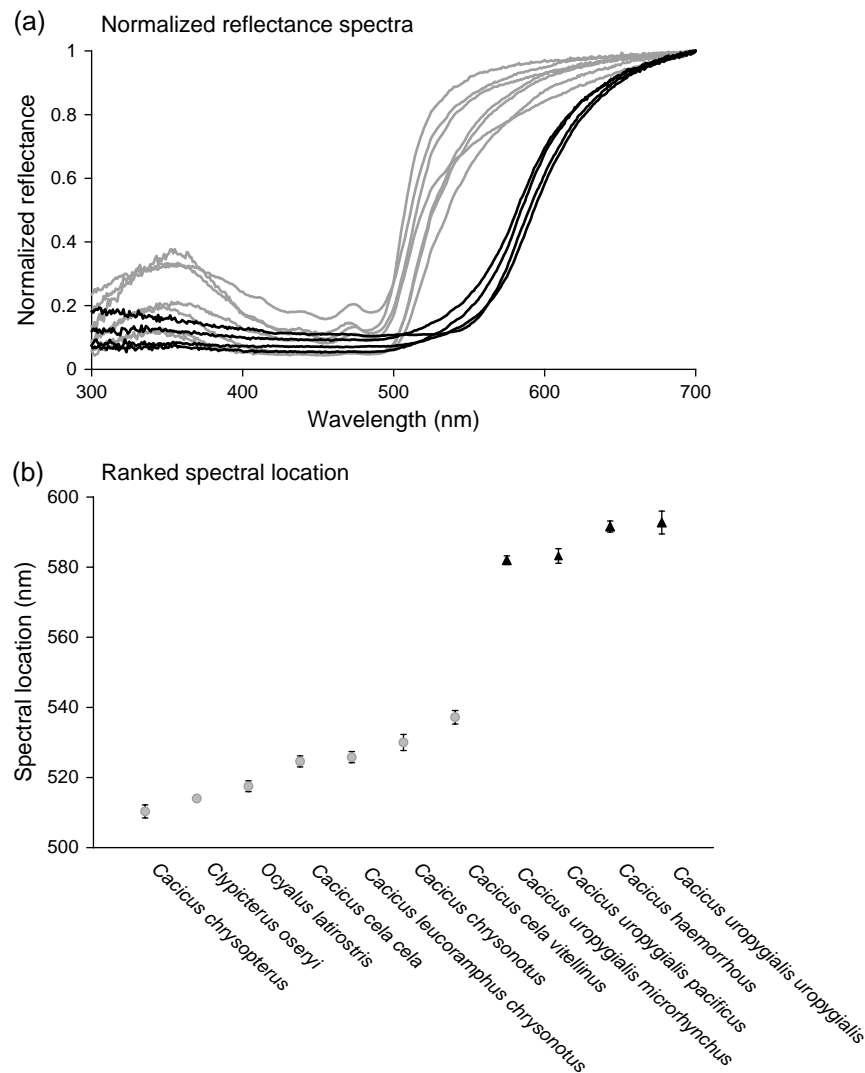


Figure 1. (a) Normalized reflectance spectra of cacique colored plumage patches. The average spectrum (from five separate measurements; see methods) for each taxon is shown. Measurements from color patches that appear yellow are shown in grey, and those from patches that appear red are shown in black. (b) Average spectral location of each taxon measured. “Yellow” taxa are shown as grey circles and “red” taxa are shown as black triangles. “Red” taxa include the three *C. uropygialis* subspecies and *C. haemorrhous*. Note that the spectral locations fall into two discrete spectral bins and that the spectral location of *C. haemorrhous* falls within the values of *C. uropygialis*. Standard error bars are shown ( $\pm 1$  SE).

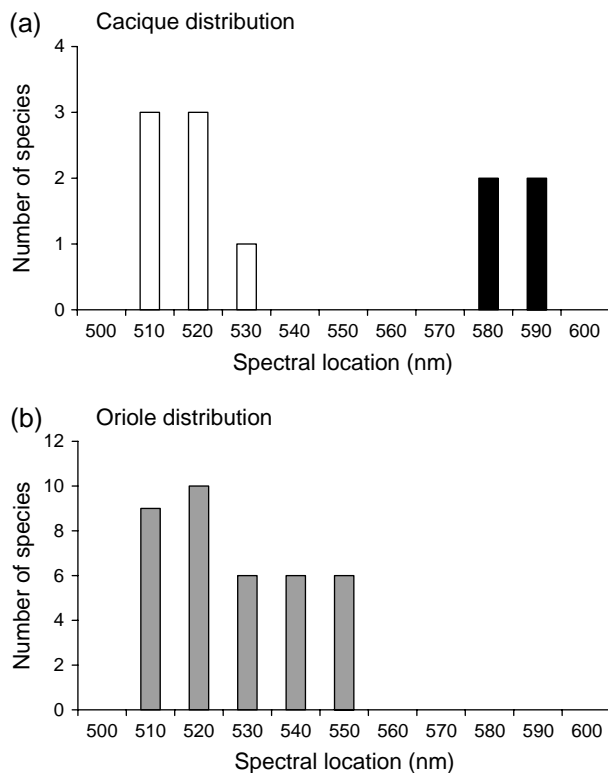


Figure 2. Histograms showing the distribution of spectral location values among extant (a) caciques, and (b) orioles. Cacique spectral location values form a bimodal distribution, while orioles form a single, broad distribution centered around middle wavelength (orange) colors. Oriole rump values were obtained from Hofmann et al. (2006).

Across all taxa, spectral location ranged from 510 to 593 nm (Fig. 1 and 2). A large jump in spectral location occurred from 537 to 582 nm. Eight taxa showed short-wavelength spectral locations, from 510 to 537 nm, whereas four taxa showed long-wavelength spectral locations, from 582 to 592 nm (Fig. 2). Within each taxon measured, we saw little variation overall and noticed no geographical clines in color. The spectral location groups correspond to the visibly distinguishable color groups; taxa in the short-wavelength group all appear yellow, and those in the long-wavelength group all appear red. The two groups were widely separated, with more than four standard deviations separating the longest wavelength “yellow” taxon from the shortest wavelength “red” taxon (using the larger yellow standard deviation; Fig. 1b). The four long-wavelength taxa include the three *C. uropygialis* subspecies, as well as *C. haemorrhous*. The spectral location of *C. haemorrhous* falls within the values of the three *uropygialis* taxa (see Fig. 1b), with spectral locations of 582, 583, 592, and 593 nm for *C. u. microrhynchus*, *C. u. pacificus*, *C. haemorrhous*, and *C. u. uropygialis*, respectively. During examination of museum collections, no adults of “red” cacique taxa were visually distinguishable as more orange than other individuals, though we did note that colored patches of some immature specimens were slightly more orange than adults. However, their spectral locations generally fell close to or within the adult range, and qualitative color difference was mostly due to changes in other aspects of color such as

brightness and saturation (unpublished data, see Jaramillo and Burke 1999 for illustrations).

## Reconstructions

Parsimony and maximum likelihood reconstructions yielded nearly identical results. Both methods suggest that the common ancestor of the group had yellow colored patches, with two independent gains of red coloration and one change to no visible carotenoid plumage (Fig. 3a). Red coloration appeared to be gained in the common ancestor of the *C. uropygialis* group (which includes the three subspecies *C. u. uropygialis*, *C. u. pacificus*, and *C. u. microrhynchus*) as well as in *C. haemorrhous*. We did not observe any reversals back to yellow.

Linear parsimony (the same continuous method that was used to reconstruct oriole coloration) also suggested a short-wavelength ancestor, two independent gains of long-wavelength colors and no intermediate-wavelength ancestors (Fig. 3b). Likewise, two independent gains of red were also supported when *C. sclateri*, *C. oseryi* and *O. latirostris* were scored black and as missing data. Only the state of the common ancestor shared by *O. latirostris*, *C. oseryi*, and *C. haemorrhous* varied significantly. When scored as black, parsimony could no longer resolve it and maximum likelihood favored a black state. When scored as missing data, neither parsimony nor maximum likelihood could resolve it.

## Discussion

### Different patterns of evolutionary change

Extant cacique carotenoid spectral locations cluster into two distinct groups: a short-wavelength group (yellow) and a long-wavelength group (red). The substantial gap in the middle wavelengths allows taxa to be clearly and non-arbitrarily grouped and suggests that in caciques, changes from short to long-wavelength colors occurred in discrete jumps. Phylogenetic reconstructions suggest that the ancestral cacique had yellow colored plumage and that two independent gains of red color have occurred (as well as one change to achromatic black plumage). The discrete variation in color that we observed in extant caciques differs from the continuous variation found in orioles. Thus, despite their relatively close phylogenetic relationship, caciques and orioles appear to have very different modes of color evolution (Fig. 2).

In addition to the contrast between caciques and orioles in terms of discrete versus continuous color evolution, another pattern emerges. Cacique coloration has been generally stable with two discontinuous changes in a single direction, whereas oriole coloration has shown higher levels of lability across the clade with multiple shifts in spectral location towards shorter- (yellow) and longer-wavelength (red) colors, as well as a wide variety of orange intermediate colors in both extant and ancestral taxa (Hofmann et al. 2006).

Sexually selected traits, such as elaborate color ornaments and song characteristics, may change particularly rapidly and are influenced by a complex ensemble of factors

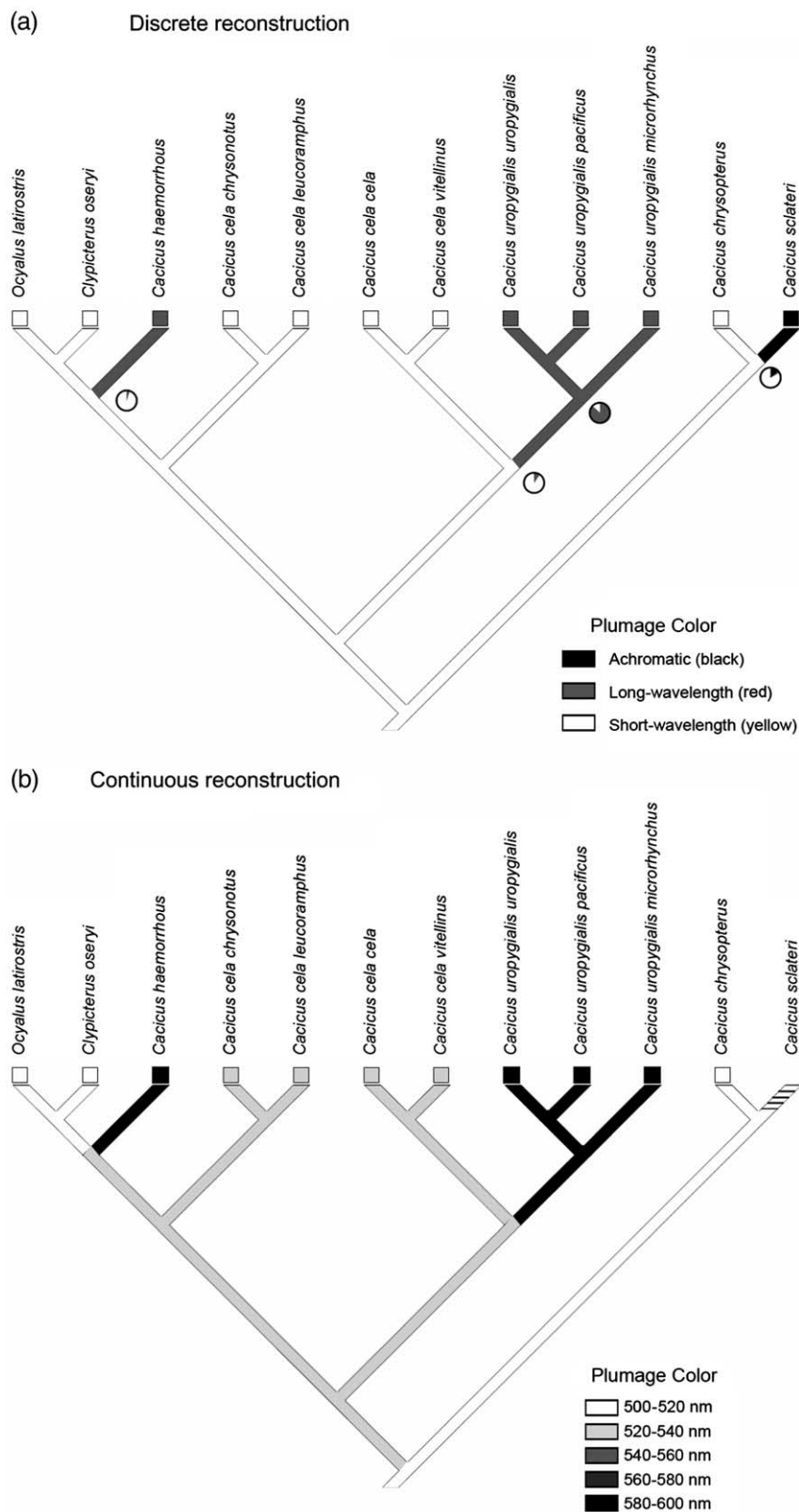


Figure 3. Ancestral state reconstruction of cacique carotenoid coloration as (a) a discrete and (b) a continuous character. (a) In the discrete reconstruction a yellow common ancestor was inferred, with two independent changes to red. Both, parsimony and maximum likelihood reconstructions yielded similar results. Branches are colored according to parsimony, and maximum likelihood probabilities are shown as pie charts at relevant nodes. Note that branch lengths were included in the maximum likelihood analysis. (b) The continuous reconstruction also favored a short-wavelength common ancestor with two independent changes to longer wavelengths and supported the lack of intermediate ancestral states. Continuous characters states were reconstructed using linear parsimony and binned for illustrative purposes only. The black plumage of *C. sclateri* could not be scored on the same continuous scale and was treated as missing data.

including female preferences, habitat characteristics, energetic costs and benefits, and other evolutionary trade-offs (Andersson 1994, Hill 2006). A revealing next step would be to rigorously score plumage patterns in the larger cacique and oropendola group (as done in orioles by Omland and Lanyon 2000) and, compare changes in cacique and oropendola song (Price and Lanyon 2004) with patterns of color evolution (as done in orioles by Price et al. 2007).

### Ultimate factors impacting color evolution

Within the caciques, there is a wide diversity of life histories, range sizes, and habitat preferences. Mating systems range from social monogamy with solitary nesting, to high polygyny with large nesting colonies; distributions vary from small, restricted ranges to distributions across much of South America; and habitat preferences range from montane forest canopies to humid lowlands (Jaramillo and Burke 1999). Carotenoid plumage evolution could be influenced by any of these factors, from intense sexual selection (especially on males in polygynous taxa) to natural selection in different habitat types (e.g., due to light environment; Endler 1993, Johnson and Lanyon 2000, Théry 2006).

Upon comparing available literature on each taxon's range, habitat, diet and life history, there is no one factor that all yellow or all red caciques have in common. However, when examining the geographic distributions of these taxa, an interesting trend arises. There are many instances of yellow caciques being sympatric with red caciques, but very little overlap among taxa of the same color (Jaramillo and Burke 1999). This lack of sympatry within color types could be explained by several interesting mechanisms. First, it could be related to species recognition, for example with these color differences evolving through reproductive character displacement (e.g., Sætre et al. 1997). Second, it could be that species that evolve color differences in allopatry are able to become sympatric (Omland and Kondo 2006). In the first mechanism, species recognition drives the evolution of color changes, whereas in the second mechanism, color changes that arise due to other causes such as sexual selection or drift, facilitate later sympatry (Omland and Kondo 2006). The role of species recognition in driving color differences, or color differences facilitating species persistence should be pursued in future behavioral studies across caciques, or future comparative studies of Icterids and other birds.

### Proximate implications of discrete color change

Although we did not chemically analyze feather pigments, one possible explanation for the discreteness of yellow and red plumage in caciques is that only one or a few pigments are involved in producing colored patches. If caciques use only one or a few pigments, a simple chemical change in one pigment type could drastically alter plumage color. Previous work has shown that even a single metabolic change in a carotenoid pigment can provoke a dramatic change in appearance (Brush 1967, 1990). For example, the

seasonal change in adult male scarlet tanagers *Piranga olivacea* from yellow non-breeding plumage to scarlet red in the breeding season is due to nothing more than a change in the oxidation state of a single side chain of a carotenoid pigment (Brush 1967, 1990). Similar changes could have occurred in cacique evolutionary history, with the resultant red plumage driven to fixation by drift or selection.

The discretely different colors of caciques can be contrasted with the continuous variation observed in the closely related oriole genus. The Baltimore oriole *Icterus galbula*, and likely several other species, use a complex mixture of at least five yellow and red carotenoid pigments. Thus, the final plumage color depends on both the identity and the relative proportion of pigments in the feather and the continuous variation observed in orioles could arise by varying the relative concentrations of each pigment (Hofmann et al. 2006). In such a system, the effect of the loss or gain of a pigment may be mitigated by redundancy.

A simple one or few-pigment mechanism in caciques could suggest that the two changes to red coloration present a case of parallel evolution, especially if the conversion between the yellow and red pigments involved were particularly chemically favorable. Both the overall spectral shapes and spectral locations for the two groups of red taxa are quite similar, with *C. haemorrhous's* spectral location falling within the range of that of the *C. uropygialis* complex (Fig. 2), and could presumably represent a change to the same red pigment. However, spectral data cannot be reliably used to identify particular pigments or pigment concentrations, and it is possible that different mechanisms are producing similar colors in these taxa. Further investigation of the pigment content of cacique and oriole feathers will provide exciting new insights into the ways in which the proximate mechanisms of color production shape the evolution of elaborate color traits.

### Discrete vs continuous evolution

Caciques and orioles present interesting case studies in the methods of coding and reconstructing ancestral characters. A wide variety of characters can be measured using methods that produce continuous data sets, from body size to song characters to spectral color data. However, just because such characters can be *measured* along a continuous scale, does not mean that these characters should be *reconstructed* using continuous methods. In caciques, the marked differences in spectral shapes and wide separation of spectral locations between "red" and "yellow" taxa strongly support the notion of discontinuous changes between yellow and red coloration. Although we also reconstructed cacique color changes using same continuous method that we used previously to examine evolutionary changes in oriole coloration (linear parsimony), we performed this analysis for comparative purposes, and were cognizant that it might not best represent the underlying proximate mechanism of change. Linear parsimony produced similar results, likely because it allows for punctuated color change (Hofmann et al. 2006). Other continuous methods, such as squared change parsimony (which is more representative of a Brownian process), would infer intermediate ancestral states

(shades of orange). Several ancestral nodes would be reconstructed as having values well outside those found in any extant species (data not shown). If indeed cacique coloration changes directly from yellow to red, these “orange” ancestral colors would never have existed, and the reconstruction is misleading. Overall, the decision to reconstruct any character as continuous or discrete is an important choice that must be based on the distribution of character states in extant taxa, and, most importantly, our best understanding of the proximate mechanisms involved in the production of the character states (Hofmann et al. 2006, 2007, Omland and Hofmann 2006).

## Summary

Caciques and orioles provide an excellent example of two closely related groups with drastically different modes of character evolution. Cacique colors vary discretely with only two character states, while oriole coloration varies continuously. Caciques likely had a yellow ancestor, with two independent gains of red coloration, one loss of visible carotenoid color, and no reversals. In contrast, orioles show multiple bidirectional changes towards shorter- (yellow) and longer-wavelength (red) colors, with extant species showing a continuous range of intermediate colors (oranges). Caciques and orioles also illustrate the importance of the assumptions used to score and reconstruct changes in character states. While this is a significant issue for any ancestral state reconstruction, it is particularly important in cases where measurement technology (e.g., reflectance spectrometry) provides continuous data regardless of the true evolutionary mode of the characters in question.

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Appendix 1. Voucher numbers and collection location for specimens measured.

| Taxon                                    | Voucher no. | Collection location     |                |            |
|--|-------------|-------------------------|----------------|------------|
|  |             | Locality                | State/province | Country    |
| <i>Ocyalus latirostris</i>               | FMC 249526  | Quebrada Esperanza      | Loreto         | Peru       |
|  | FMC 283723  | Obrero                  | Loreto         | Peru       |
|  | FMC 283724  | Obrero                  | Loreto         | Peru       |
|  | FMC 296788  | Bosque Zapatogocha      | Huanuco        | Peru       |
| <i>Clypicterus oseryi</i>                | FMC 187731  | Previsto                | Ucayali        | Peru       |
|  | FMC 208363  | Balceadero              | Cusco          | Peru       |
|  | FMC 208364  | Balceadero              | Cusco          | Peru       |
|  | FMC 252213  | Rio de las Piedras      | Madre de Dios  | Peru       |
|  | NMNH 308924 | Puerto Indiana          | Loreto         | Peru       |
| <i>Cacicus haemorrhous</i>               | NMNH 60601  | –                       | –              | Brazil     |
|  | NMNH 335213 | Faz Da Guarany          | –              | Brazil     |
|  | NMNH 368453 | Colatina                | Espirito Santo | Brazil     |
|  | NMNH 368454 | Pau Gigante, Da Sede    | Espirito Santo | Brazil     |
|  | NMNH 515907 | Santa Barbara Benevides | Para           | Brazil     |
| <i>Cacicus chrysonotus chrysonotus</i>   | FMC 153178  | Oconeque                | Puno           | Peru       |
|  | FMC 208377  | Hacienda Cadena         | Cusco          | Peru       |
|  | FMC 217810  | Choro                   | Cochabamba     | Bolivia    |
|  | FMC 217812  | Choro                   | Cochabamba     | Bolivia    |
|  | NMNH 273476 | Torontoy                | Cusco          | Peru       |
| <i>Cacicus leucoramphus</i>              | FMC 299803  | Bosque San Luis         | Cusco          | Peru       |
|  | NMNH 256302 | El Eden, Andes          | Quindio        | Colombia   |
|  | NMNH 412638 | Hacienda Las Vegas      | Santander      | Colombia   |
|  | NMNH 436985 | Rio Urrao               | Antioquia      | Colombia   |
|  | NMNH 444754 | Paletera                | Cauca          | Colombia   |
| <i>Cacicus cela cela</i>                 | NMNH 316605 | Puerto Ayacucho         | Amazonas       | Venezuela  |
|  | NMNH 325155 | Santa Maria             | Miranda        | Venezuela  |
|  | NMNH 369991 | Carraipia               | La Guajira     | Colombia   |
|  | NMNH 514537 | Belem, Utinga           | Para           | Brazil     |
|  | NMNH 515279 | Rio Tracajatuba         | Amapa          | Brazil     |
| <i>Cacicus cela vitellinus</i>           | NMNH 32003  | Panama Rail Road        | –              | Panama     |
|  | NMNH 53919  | –                       | –              | Panama     |
|  | NMNH 236678 | Chorrera                | San Blas       | Panama     |
|  | NMNH 374953 | Codazzi                 | Magdalena      | Colombia   |
|  | NMNH 427398 | Nicocli                 | Antioquia      | Colombia   |
| <i>Cacicus uropygialis uropygialis</i>   | FMC 99636   | Bermejo                 | Napo           | Ecuador    |
|  | FMC 190021  | Chanhamayo              | Junín          | Peru       |
|  | FMC 283727  | Yurinaqui Alto          | Junín          | Peru       |
|  | FMC 299801  | Bosque Udina            | Amazonas       | Peru       |
| <i>Cacicus uropygialis pacificus</i>     | NMNH 256308 | Alto Bonito             | Antioquia      | Colombia   |
|  | NMNH 386518 | Jaque                   | Darien         | Panama     |
|  | NMNH 412639 | Quebrada Salvajin       | Cordoba        | Colombia   |
|  | NMNH 436894 | Rio Samana              | Caldas         | Colombia   |
|  | NMNH 443751 | Nuqui                   | Choco          | Colombia   |
| <i>Cacicus uropygialis microrhynchus</i> | NMNH 198989 | Bonilla                 | Limon          | Costa Rica |
|  | NMNH 207297 | Lion Hill               | Colon          | Panama     |
|  | NMNH 469141 | Almirante               | Bocas Del Toro | Panama     |
|  | NMNH 474714 | Juan Mina Guayabalito   | Canal Zone     | Panama     |
|  | NMNH 533306 | Puerto Armuelles, Olivo | Chiriqui       | Panama     |
| <i>Cacicus chrysopterus</i>              | NMNH 284274 | Puerto Pinasco          | Concepción     | Paraguay   |
|  | NMNH 284277 | Riacho Pilaga           | Formosa        | Argentina  |
|  | NMNH 350824 | Serra Do Itatiaya       | Rio De Janeiro | Brazil     |

Museums are abbreviated as follows: NMNH, Smithsonian National Museum of Natural History; FMC, Field Museum in Chicago.